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Productivity of epibenthic species : a review

F. Redant

Fisheries Research Station
Ankerstraat 1, B-8400 Oostende, Belgium

Abstract

A review of bibliographic data on the productivity (production : biomass ratios) of makrobenthos from the NW and NE Atlantic, with emphasis on epi- and hyperbenthos, is presented. It consists of about 160 data sets on almost 100 different species. The P/B ratios of epi- and hyperbenthos range from 0.1 to 9.3 and compare to those reported for the macroendofauna.

Résumé

Une revue synoptique sur la productivité (le rapport production : biomasse) du macrobenthos de l'Atlantique du Nord, avec l'accent sur la faune épi- et hyperbenthique, est présentée. Elle consiste d'environ 160 séries de données sur presque 100 espèces différentes. Les rapports P/B pour les espèces épi- et hyperbenthiques vont de 0.1 à 9.3 et sont comparables à ceux pour la faune endobenthique.

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1. Introduction

Over the last decades the scientific community has become increasingly aware of the importance of productivity studies on benthic organisms.

Reliable estimates of the production by the different compartments of the benthic community are essential to our understanding of the energy flow through the benthos, and from the benthos to demersal fish. They are equally important when assessing the impact of natural or man-made perturbations of the sea-bed, or when tracing the likely pathways of toxic substances through the benthic-demersal food chain.

In view of these arguments the Benthos Ecology Working Group, during its 1986 meeting, agreed to collate and to re-evaluate the existing data on the productivity of benthic organisms.

The meiobenthos data were reviewed in a comprehensive paper by HEIP and HERMAN (1988), whereas BREY (1989) discussed some general aspects of the relationships between production, productivity, biomass and mean individual weight of macro- and epibenthos.

The present paper reviews more precisely the productivity figures for epi- and hyperbenthic species in the NE and NW Atlantic.

2. Review of epibenthos productivity data

The definitions of epi- and hyperbenthos were taken in their strict ecological sense, i.e. all animals living on the sea-bed, either attached or crawling (epibenthos), or swimming, for the most during part of the day, in the water column just above the sea-bed (hyperbenthos).

The epi- and hyperbenthos comprises various taxonomic groups, such as sponges, anthozoans, some bivalve and most gastropod molluscs, bryozoans, some crustaceans (e.g. decapods, some isopods, amphipods, mysids, etc.), most echinoderms, tunicates and some small, bottom-dwelling fish (e.g. gobiids).

Several of these species (e.g. shrimps, crabs and gobiids) figure among the major food items of demersal fish, particularly gadoids. Others, such as mussels, oysters, scallops, shrimps, crabs and lobsters, are important aquaculture and fishery resources.

The productivity data (given as production : biomass or P/B

ratios) for epi- and hyperbenthic organisms are summarized in Table 1.

Apart from evident items, such as area of investigations and bibliographic reference, the table also contains information on the methods used to estimate biomass and production, the time-span over which mean biomass and overall production were measured or calculated, and the type of units used to express biomass and production (weight units or energy equivalents).

For comparison the P/B ratios of macro-endobenthic species are listed in Table 2, albeit in a slightly more condensed form (species, area of investigations, time-span, P/B ratio and reference only).

Whenever possible the P/B ratios were checked against the original production and biomass figures given by the authors. Single ratios were rounded to the nearest 0.05 and ranges to the nearest 0.1.

Table 1 comprises about 50 data sets for 29 epi- and hyperbenthic species : one cumacean, six decapods, two isopods, two mysids, one asteroid, one echinoid, five ophiuroids, four bivalves, four gastropods and three gobiid fish.

Table 2 comprises 110 data sets for almost 70 macro-endobenthic species : 27 polychaetes, five amphipods, one isopod, three echinoids, one echiurid, 30 bivalves and one priapulid.

Some of the data in Tables 1 and 2 already were reviewed by GREZE (1978). Unfortunately however, GREZE's summary tables appeared to contain a large number of 'misprints'. Some of the P/B ratios in his Table 3.3. in fact are B/P ratios, which explains at least part of the discrepancy in the data sets for a number of species.

It is quite surprising that, in spite of their economical importance, very little or even no productivity data at all are available for oysters, scallops, shrimps (except for Crangon), larger crabs and lobsters. Numerous studies have dealt with the 'production' of these species in terms of yield to the fisheries, but for obvious reasons such estimates cover only part of their actual production. The same holds for the estimates of their 'stock biomass', which usually refer to the exploitable part only of these populations.

The P/B ratios of epi- and hyperbenthic animals range from 0.1 (Calocaris macandreae, Northumberland and Mytilis edulis, West Greenland) to 9.3 (Crangon crangon, Dutch Wadden Sea). Most crustaceans and the gobiids appear to be in the top half of the range, with P/B ratios exceeding 2.0 ; most molluscs are in the lower half, with P/B ratios below 2.0 and even

well below 1.0, and most echinoderms are in the middle part of the range, with P/B ratios between 0.5 and 2.5 (Table 1).

Both the range and the distribution of the P/B ratios for epibenthic species compare to those for the macro-endofauna (Tables 1 and 2).

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Table 1. - P/B ratios of epi- and hyperbenthos (1).

Crustacea - Cumacea

Species : DIASTYLIS RATHKEI
 Area : NE Atlantic, England, Swansea Bay
 Methods - B : Day grab - 0.5 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 1.25
 Reference : Warwick and George (1980)

Species : DIASTYLIS RATHKEI
 Area : North Sea, Germany, German Bight
 Methods - B : Van Veen and Reineck - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 3.25
 Reference : Rachor, Arntz, Rumohr and Mantau (1982)

Species : DIASTYLIS RATHKEI
 Area : Baltic Sea, Germany, Kiel Bay
 Methods - B : Van Veen grab - 0.9 mm sieve
 - P : difference between B_{max} and B_{min}
 Period : year
 Units : weight units
 P/B ratio : 1.00
 Reference : Arntz (1971)
 Comments : minimal estimates of production and P/B ratio

Species : DIASTYLIS RATHKEI
 Area : Baltic Sea, Germany, Kiel Bay
 Methods - B : Van Veen and Reineck - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 2.65
 Reference : Rachor, Arntz, Rumohr and Mantau (1982)

Table 1. - P/B ratios of epi- and hyperbenthos (3).

Crustacea - Decapoda (cont.)

Species : CRANGON CRANGON
 Area : North Sea, Netherlands, Wadden Sea
 Methods - B : small meshed beam trawl
 - P : from P/C ratio
 Period : year
 Units : weight units
 P/B ratio : 9.20 (P/B ratio overestimated, real value assumed to be \approx 7.0)
 Reference : Van Lissa (1977)

Species : CRANGON CRANGON
 Area : North Sea, Netherlands, Wadden Sea
 Methods - B : small meshed beam trawl
 - P : from changes in biomass and Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : ranging from 7.7 to 9.3
 Reference : Kuipers and Dapper (1981)

Species : CRANGON CRANGON
 Area : Baltic Sea, Sweden, Skagerrak
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : 8 months
 Units : weight units
 P/B ratio : 2.00 (0-group only - calculated from original P and B figures given by the authors)
 Reference : Baden and Pihl (1984)

Species : CRANGON CRANGON
 Area : Baltic Sea, Sweden, Skagerrak, Kattegat
 Methods - B : drop trap
 - P : from growth and population composition data
 Period : year
 Units : weight units
 P/B ratio : 5.40
 Reference : Möller, Pihl and Rosenberg (1985)

Species : CRANGON CRANGON
 Area : Baltic Sea, Sweden, Skagerrak, Kattegat
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 0-group 2.2 and I-group 2.1
 Reference : Pihl (1986)

Table 1. - P/B ratios of epi- and hyperbenthos (4).

Crustacea - Decapoda (cont.)

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Species      : CRANGON SEPTemspINOSA
Area         : NW Atlantic, USA, Long Island
Methods - B  :
            - P :
Period       : year
Units        :
P/B ratio    : 3.65
Reference    : Richards and Riley (1967) in Greze (1978)

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Species : PALAEMON ADSPERSUS
Area : Baltic Sea, Sweden, Skagerrak
Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
Period : 8 months
Units : weight units
P/B ratio : ranging from 1.4 to 1.8 (different locations-
 calculated from original P and B figures given
 by the authors)
Reference : Baden and Pihl (1984)

Species : PALAEMON ELEGANS
Area : Baltic Sea, Sweden, Skagerrak
Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
Period : 8 months
Units : weight units
P/B ratio : 1.60 (calculated from original P and B figures
 given by the authors)
Reference : Baden and Pihl (1984)

Table 1. - P/B ratios of epi- and hyperbenthos (5).

Crustacea - Isopoda

Species : IDOTEA BALTICA
 Area : Baltic Sea, Sweden, Skagerrak
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : 8 months
 Units : weight units
 P/B ratio : 3.00 (0-group only - calculated from original
 P and B figures given by the authors)
 Reference : Baden and Pihl (1984)

Species : IDOTEA VIRIDIS
 Area : Baltic Sea, Sweden, Skagerrak
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : 8 months
 Units : weight units
 P/B ratio : ranging from 1.5 to 1.7 (different locations-
 calculated from original P and B figures given
 by the authors)
 Reference : Baden and Pihl (1984)

Crustacea - Mysidacea

Species : GASTROSACCUS SPINIFER
 Area : Baltic Sea, Germany, Kiel Bay
 Methods - B : Van Veen grab - 0.9 mm sieve
 - P : difference between B_{max} and B_{min}
 Period : year
 Units : weight units
 P/B ratio : 1.10
 Reference : Arntz (1971)
 Comments : minimal estimates of production and P/B ratio

Species : NEOMYSIS AMERICANA
 Area : NW Atlantic, USA, Long Island
 Methods - B :
 - P :
 Period : year
 Units :
 P/B ratio : 3.65
 Reference : Richards and Riley (1967) in Greze (1978)

Table 1. - P/B ratios of epi- and hyperbenthos (6).

Echinodermata - Asteroidea

Species : ASTERIAS FORBESI
Area : NW Atlantic, USA, Long Island
Methods - B :
 - P :
Period : year
Units :
P/B ratio : 8.40
Reference : Richards and Riley (1967) in Greze (1978)

Echinodermata - Echinoidea

Species : STRONGYLOCENTROTUS DROEBACHIENSIS
Area : NW Atlantic, Canada, Nova Scotia
Methods - B : scuba diving
 - P : from in vitro experiments
Period : year
Units : energy equivalents
P/B ratio : 0.80
Reference : Miller and Mann (1973)

Species : STRONGYLOCENTROTUS DROEBACHIENSIS
Area : NW Atlantic, Canada, Nova Scotia
Methods - B : scuba diving
 - P : McNeill and Lawton (1970) (modified)
Period : year
Units : energy equivalents
P/B ratio : 0.80
Reference : Miller, Mann and Scarratt (1971)

Echinodermata - Ophiuroidea

Species : AMPHIOPLUS CONIORTODES
Area : NW Atlantic, USA, Biscayne Bay
Methods - B : grab (type not specified)
 - P : from growth and population composition data
Period : year
Units : weight units
P/B ratio : 2.25
Reference : Moore (1972)

Table 1. - P/B ratios of epi- and hyperbenthos (7).

Echinodermata - Ophiuroidea (cont.)

Species : OPHIONEPTHYS LIMICOLA
 Area : NW Atlantic, USA, Biscayne Bay
 Methods - B : grab (type not specified)
 - P : from growth and population composition data
 Period : year
 Units : weight units
 P/B ratio : 2.35
 Reference : Moore (1972)

Species : OPHIOTHRIX FRAGILIS
 Area : NE Atlantic, England, Bristol Channel
 Methods - B : Day grab - 0.5 mm sieve
 - P : cohort growth analysis
 Period : year
 Units : weight units
 P/B ratio : 1.80
 Reference : George and Warwick (1985)

Species : OPHIURA ALBIDA
 Area : Baltic Sea, Germany, Kiel Bay
 Methods - B : Van Veen grab - 0.9 mm sieve
 - P : difference between B_{max} and B_{min}
 Period : year
 Units : weight units
 P/B ratio : 0.80
 Reference : Arntz (1971)
 Comments : minimal estimates of production and P/B ratio

Species : OPHIURA TEXTURATA
 Area : NE Atlantic, England, Swansea Bay
 Methods - B : Day grab - 0.5 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 0.50
 Reference : Warwick and George (1980)

Species : OPHIURA TEXTURATA
 Area : NE Atlantic, England, Carmarthen Bay
 Methods - B : Knudsen and Day grabs - 0.5 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 0.70
 Reference : Warwick, George and Davies (1978)

Table 1. - P/B ratios of epi- and hyperbenthos (8).

Mollusca - Bivalvia

Species : CHLAMYS VARIA
 Area : NE Atlantic, France, Bay of Brest
 Methods - B :
 - P :
 Period : year
 Units :
 P/B ratio : ranging from 0.4 to 0.5 (different years)
 Reference : Shafee and Conan (1984)

Species : CRASSOSTREA VIRGINICA
 Area : NW Atlantic, USA, South Carolina
 Methods - B : intertidal transects and rectangles
 - P : from growth and mortality data
 Period : year
 Units : energy equivalents
 P/B ratio : 2.0 (including spawn) or 1.7 (excluding spawn)
 Reference : Dame (1976)

Species : MODIOLUS DEMISSUS
 Area : NW Atlantic, USA, Georgia
 Methods - B :
 - P :
 Period : year
 Units :
 P/B ratio : 0.28
 Reference : Kuenzler (1961) in Dame (1976)

Species : MYTILUS EDULIS
 Area : NW Atlantic, West Greenland, Disko Bugt
 Methods - B : Van Veen grab - 1.0 mm sieve
 - P : from growth and mortality data
 Period : year
 Units : weight units
 P/B ratio : 0.10
 Reference : Petersen (1978)

Species : MYTILUS EDULIS
 Area : Irish Sea, England, Morecambe Bay
 Methods - B : intertidal core samples - several mesh sizes
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : ranging from 1.7 to 4.4 (different years)
 Reference : Dare (1976)

Table 1. - P/B ratios of epi- and hyperbenthos (10).

Mollusca - Gastropoda

Species : CREPIDULA FORNICATA
 Area : North Sea, Netherlands, Grevelingen
 Methods - B : Van Veen and corer - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : ranging from 0.2 to 1.4 (different years and locations)
 Reference : Wolff, Vegter, Mulder and Meijs (1976)

Species : HYDROBIA ULVAE
 Area : North Sea, Netherlands, Grevelingen
 Methods - B : Van Veen and corer - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : ranging from 1.2 to 1.8 (different locations)
 Reference : Wolff and de Wolf (1977)

Species : HYDROBIA ULVAE
 Area : North Sea, Germany, German Bight, Sylt
 Methods - B : corer
 - P : from changes in mean individual weight
 Period : year
 Units : weight units
 P/B ratio : 1.25
 Reference : Asmus (1982)

Species : LITTORINA LITTOREA
 Area : North Sea, Netherlands, Grevelingen
 Methods - B : Van Veen and corer - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : ranging from 0.4 to 0.6 (different locations)
 Reference : Wolff and de Wolf (1977)

Species : LITTORINA SAXATILIS
 Area : NW Atlantic, Canada, Nova Scotia
 Methods - B : intertidal transects and rectangles
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : mean 4.10, ranging from 2.9 to 5.1 (different age groups)
 Reference : Burke and Mann (1974)

Table 1. - P/B ratios of epi- and hyperbenthos (11).

Pisces - Osteichthyes

Species : GOBIUS NIGER
 Area : Baltic Sea, Sweden, Skagerrak
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : 8 months
 Units : weight units
 P/B ratio : 0-group \approx 1.0 (calculated from original P and B figures given by the authors)
 Reference : Baden and Pihl (1984)

Species : POMATOSCHISTUS MICROPS
 Area : North Sea, Netherlands, Grevelingen
 Methods - B : small meshed beam trawl
 - P : not specified
 Period : 7 months
 Units : weight units
 P/B ratio : 3.20
 Reference : Erenst and De Graaf (1982)

Species : POMATOSCHISTUS MICROPS
 Area : Baltic Sea, Sweden, Skagerrak, Kattegat
 Methods - B : drop trap
 - P : from growth and population composition data
 Period : year
 Units : weight units
 P/B ratio : 3.00
 Reference : Möller, Pihl and Rosenberg (1985)

Species : POMATOSCHISTUS MICROPS
 Area : Baltic Sea, Sweden, Skagerrak, Kattegat
 Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
 Period : year
 Units : weight units
 P/B ratio : 2.20 (0-group only)
 Reference : Pihl (1986)

Species : POMATOSCHISTUS MINUTUS
 Area : Baltic Sea, Sweden, Skagerrak, Kattegat
 Methods - B : drop trap
 - P : from growth and population composition data
 Period : year
 Units : weight units
 P/B ratio : 2.90
 Reference : Möller, Pihl and Rosenberg (1985)

Table 1. - P/B ratios of epi- and hyperbenthos (12).

Pisces - Osteichthyes (cont.)

Species : POMATOSCHISTUS MINUTUS
Area : Baltic Sea, Sweden, Skagerrak, Kattegat
Methods - B : drop trap - 1.0 mm sieve
 - P : Crisp (1971)
Period : year
Units : weight units
P/B ratio : 2.00 (0-group only)
Reference : Pihl (1986)

Table 2. - P/B ratios of macro-endofauna (1).

Annelida - Polychaeta

Ammotrypane aulogaster	North Sea, England, Northumberland	year	2.05		Buchanan and Warwick (1974)
Ampharete acutifrons	NW Atlantic, USA, Long Island	year	4.60		Richards and Riley (1967) in Heip and Herman (1979)
Ampharete acutifrons	NE Atlantic, England, Swansea Bay	year	1.30		Warwick and George (1980)
Ampharete acutifrons	NE Atlantic, England, Cornwall	year	5.45		Warwick and Price (1975)
Ampharete acutifrons	NE Atlantic, England, Cornwall	year	5.45		Warwick, Joint and Radford (1979)
Arenicola marina	NE Atlantic, France, Roscoff	year	0.7-1.5	(e)	Pollack (1979)
Arenicola marina	North Sea, Netherlands, Grevelingen	year	0.7-1.1	(d)	Wolff and de Wolf (1977)
Arenicola marina	North Sea, Netherlands, Wadden Sea	year	≈ 1.00 ≈ 0.65	(a) (b)	Beukema and de Vlas (1979)
Chaetozone setosa	North Sea, England, Northumberland	year	1.30		Buchanan and Warwick (1974)
Cistenoides gauldii	NW Atlantic, USA, Long Island	year	1.90		Sanders (1956) in Heip and Herman (1979)
Glycera alba	NE Atlantic, England, Carmarthen Bay	year	0.95		Warwick, George and Davies (1978)

Table 2. - P/B ratios of macro-endofauna (2).

Annelida - Polychaeta (cont.)

Glycera rouxi	North Sea, England, Northumberland	year	0.35	Buchanan and Warwick (1974)
Harmothoe imbricata		year	2.60	Zaika (1971) in Heip and Herman (1979)
Harmothoe lunulata	NE Atlantic, England, Bristol Channel	year	1.95	George and Warwick (1985)
Harmothoe sarsi	Baltic Sea, Sweden, Aksö-Landsort	year	2.00 0.6-3.4 (c)	Cederwall (1977)
Harmothoe sarsi	Baltic Sea, Germany, Kiel Bay	year	2.00 (h)	Arntz (1971)
Heteromastus filiformis	North Sea, England, Northumberland	year	1.00	Buchanan and Warwick (1974)
Jasminiera elegans	NE Atlantic, England, Bristol Channel	year	0.35	George and Warwick (1985)
Lepidonotus squamatus	NE Atlantic, England, Bristol Channel	year	1.90	George and Warwick (1985)
Lumbrineris fragilis	North Sea, England, Northumberland	year	1.35	Buchanan and Warwick (1974)
Megalona papillicornis	NE Atlantic, England, Carmarthen Bay	year	1.10	Warwick, George and Davies (1978)
Nephtys hombergi	NE Atlantic, England, Swansea Bay	year	0.80	Warwick and George (1980)

Table 2. - P/B ratios of macro-endofauna (3).

Annelida - Polychaeta (cont.)

Nephtys hombergi	NE Atlantic, England, Cornwall	year	1.85		Warwick and Price (1975)
Nephtys hombergi	NE Atlantic, England, Cornwall	year	1.85		Warwick, Joint and Radford (1979)
Nephtys hombergi	Engl. Channel, England, Southampton	year	1.6-2.9		Oyenekan (1986)
Nephtys hombergi	Baltic Sea, Denmark, Isefjord	year	1.75		Kirkegaard (1978)
Nephtys incisa	NW Atlantic, USA, Long Island	year	2.20		Sanders (1956) in Heip and Herman (1979)
Nephtys spp.	Baltic Sea, Germany, Kiel Bay	year	1.00	(h)	Arntz (1971)
Nereis diversicolor	North Sea, Scotland, Ythan Estuary	year	3.00	(a)	Chambers and Milne (1975)
Nereis diversicolor	North Sea, Belgium, Dievengat (land-locked)	year	2.55		Heip and Herman (1979)
Nereis diversicolor	Baltic Sea, Sweden, Skagerrak	year	3.5-5.9	(g)	Möller (1985)
Nereis diversicolor	Denmark, Norsminde Fjord	year	2.60 4.50	 (g)	Kristensen (unpublished) in Möller (1985)
Nereis spp.	Baltic Sea, Sweden, Skagerrak, Kattegat	year	2.70		Möller, Pihl and Rosenberg, (1985)

Table 2. - P/B ratios of macro-endofauna (4).

Annelida - Polychaeta (cont.)

Nereis virens	North Sea, England, Thames Estuary	year	1.60		Kay and Brafield (1973)
Pectinaria hyperborea	NW Atlantic, Canada, Nova Scotia	year	4.3-4.6		Peer (1970)
Pectinaria koreni	NE Atlantic, England, Swansea Bay	year	2.10		Warwick and George (1980)
Pectinaria koreni	Baltic Sea, Denmark, Isefjord	year	3.10		Kirkegaard (1978)
Pectinaria koreni	Baltic Sea, Germany, Kiel Bay	year	3.00	(h)	Arntz (1971)
Sabellaria spinulosa	NE Atlantic, England, Bristol Channel	year	0.15		George and Warwick (1985)
Sigalion mathildae	NE Atlantic, England, Carmarthen Bay	year	0.45		Warwick, George and Davies (1978)
Spiophanes bombyx	NE Atlantic, England, Swansea Bay	year	1.30		Warwick and George (1980)
Spiophanes bombyx	NE Atlantic, England, Carmarthen Bay	year	4.85		Warwick, George and Davies (1978)
Spiophanes kroyeri	North Sea, England, Northumberland	year	1.40		Buchanan and Warwick (1974)
Syllis armillaris	NE Atlantic, England, Bristol Channel	year	0.45		George and Warwick (1985)

Table 2. - P/B ratios of macro-endofauna (5).

Annelida - Polychaeta (cont.)

Tharyx marioni	NE Atlantic, England, Carmarthen Bay	year	0.80	Warwick, George and Davies (1978)
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Crustacea - Amphipoda

Ampelisca brevicornis	North Sea, Germany, Helgoland Bight	year	3.4-4.4 (c)	Klein, Rachor and Gerlach (1975)
Corophium insidiosum	Baltic Sea, Denmark, Isefjord	4 months	1.8-4.9 (d)	Birklund (1977)
Corophium volutator	North Sea, England, Thames Estuary	year	7.70	Mossman (1977) in Möller and Rosenberg (1982)
Corophium volutator	Baltic Sea, Sweden, Skagerrak	2 gener.	5.1-11.3 (e)	Möller and Rosenberg (1982)
Corophium volutator	Baltic Sea, Sweden, Skagerrak, Kattegat	year	11.30	Möller, Pihl and Rosenberg (1985)
Corophium volutator	Baltic Sea, Denmark, Isefjord	4 months	3.2-4.4 (d)	Birklund (1977)
Pantoporeia affinis	Baltic Sea, Sweden, Aksö-Landsort	year	1.90 1.2-2.6 (c)	Cederwall (1977)
Pantoporeia femorata	Baltic Sea, Sweden, Aksö-Landsort	year	1.50 0.8-2.1 (c)	Cederwall (1977)

Table 2. -- P/B ratios of macro-endofauna (6).

Crustacea - Isopoda

Anthura gracilis	NE Atlantic, England, Bristol Channel	year	0.15	(i)	George and Warwick (1985)
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Echinodermata - Echinoidea

Brissopsis lyrifer	North Sea, England, Northumberland	year	0.30		Buchanan and Warwick (1974)
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Echinocardium cordatum	NE Atlantic, England, Carmarthen Bay	year	3.75	(g)	Warwick, George and Davies (1978)
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Moira atropos	NW Atlantic, USA, Biscayne Bay	year	0.80		Moore (1972)
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Echiurida

Echiurus echiurus	North Sea, Germany, German Bight	year	1.3-2.9	(d)	Rachor and Bartel (1981)
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Mollusca - Bivalvia

Abra alba	NE Atlantic, England, Swansea Bay	year	1.35		Warwick and George (1980)
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Abra alba	Baltic Sea, Germany, Kiel Bay	year	1.60	(h)	Arntz (1971)
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Table 2. - P/B ratios of macro-endofauna (7).

Mollusca - Bivalvia (cont.)

Abra nitida	North Sea, England, Northumberland	year	1.10		Buchanan and Warwick (1974)
Anodontia alba	NW Atlantic, USA, Biscayne Bay	year	1.80		Moore (1972)
Cerastoderma edule	NE Atlantic, England, Cornwall	year	0.25	(g)	Warwick and Price (1975)
Cerastoderma edule	NE Atlantic, England, Cornwall	year	0.25		Warwick, Joint and Radford (1979)
Cerastoderma edule	Engl.Channel, England, Southampton	year	1.1-2.6		Hibbert (1976)
Cerastoderma edule	North Sea, Netherlands, Grevelingen	year	0.8-15.2	(e)	Wolff, Vegter, Mulder and Meijs (1976)
Cerastoderma edule	North Sea, Netherlands, Grevelingen	year	0.7-8.9	(d)	Wolff and de Wolf (1977)
Cerastoderma edule	Baltic Sea, Sweden, Skagerrak	year	2.2-21.0	(eg)	Möller and Rosenberg (1983)
Cerastoderma edule	Baltic Sea, Sweden, Skagerrak, Kattegat	year	19.60		Möller, Pihl and Rosenberg (1985)
Cultellus pellucidus	North Sea, Germany, German Bight	year	≈ 1.5		Salzwedel (1980) (estimated from bibliographic data)
Cyprina islandica	Baltic Sea, Germany, Kiel Bay	year	0.85	(h)	Arntz (1971)

Table 2. - P/B ratios of macro-endofauna (8).

Mollusca - Bivalvia (cont.)

Donax vittatus	NE Atlantic, England, Carmarthen Bay	year	2.10		Warwick, George and Davies (1978)
Dosinia elegans	NW Atlantic, USA, off Miami	year	2.80		Moore and Lopez (1970) in Greze (1978)
Ensis siliqua	NE Atlantic, England, Carmarthen Bay	year	0.25		Warwick, George and Davies (1978)
Hiatella byssifera	NW Atlantic, Greenland, Disko Bugt	year	0.15		Petersen (1978)
Macoma balthica	NW Atlantic, Canada, Nova Scotia	year	1.55 1.7-2.1	(f)	Burke and Mann (1974)
Macoma balthica	NW Atlantic, Canada, Bay of Fundy	year	0.4-1.2 0.3-0.7	(d) (f)	Cranford, Peer and Gordon (1985)
Macoma balthica	NE Atlantic, England, Cornwall	year	0.90		Warwick and Price (1975)
Macoma balthica	NE Atlantic, England, Cornwall	year	0.90		Warwick, Joint and Radford (1979)
Macoma balthica	North Sea, Netherlands, Grevelingen	year	0.3-1.9	(d)	Wolff and de Wolf (1977)
Macoma balthica	North Sea, Netherlands, Wadden Sea	year	0.70		Beukema (1981) in Cranford, Peer and Gordon (1985)
Macoma calcarea	NW Atlantic, Greenland, Disko Bugt	year	0.20		Petersen (1978)

Table 2. - P/B ratios of macro-endofauna (9).

Mollusca - Bivalvia (cont.)

Mercenaria mercenaria	Engl.Channel, England, Southampton	year	0.2-0.5		Hibbert (1976)
Mercenaria mercenaria	Engl.Channel, England, Southampton	year	0.40 ≈ 0-4.3	(f)	Hibbert (1977)
Mya arenaria	NW Atlantic, Canada, Nova Scotia	year	2.55 2.5-2.8	(f)	Burke and Mann (1974)
Mya arenaria	NE Atlantic, England, Cornwall	year	0.50		Warwick and Price (1975)
Mya arenaria	NE Atlantic, England, Cornwall	year	0.50		Warwick, Joint and Radford (1979)
Mya arenaria	Baltic Sea, Sweden, Skagerrak	year	2.0-13.5	(eg)	Möller and Rosenberg (1983)
Mya arenaria	Baltic Sea, Sweden, Skagerrak, Kattegat	year	11.40		Möller, Pihl and Rosenberg (1985)
Mya arenaria	Baltic Sea, Denmark, Roskilde Fjord	year	0.60		Munch-Petersen (1973)
Mya truncata	NW Atlantic, Greenland, Disko Bugt	year	0.2-0.4	(d)	Petersen (1978)
Nucula nitidosa	North Sea, Germany, German Bight	year	1.4 0.6	(a) (b)	Rachor (1976)
Nucula nitidosa	North Sea, Germany, German Bight	year	1.40 0.9-1.8	(a) (a)	Rachor and Salzwedel (1976)

Table 2. - P/B ratios of macro-endofauna (10).

Mollusca - Bivalvia (cont.)

<i>Nucula turgida</i>	NE Atlantic, England, Swansea Bay	year	0.50	Warwick and George (1980)
<i>Pandora gouldiana</i>	NW Atlantic, USA, Long Island	year	2.00	Sanders (1956) in Greze (1978)
<i>Pharus legumen</i>	NE Atlantic, England, Carmarthen Bay	year	0.55	Warwick, George and Davies (1978)
<i>Scrobicularia plana</i>	NE Atlantic, England, Cornwall	year	0.20	Warwick and Price (1975)
<i>Scrobicularia plana</i>	NE Atlantic, England, Cornwall	year	0.25	Warwick, Joint and Radford (1979)
<i>Serripes groenlandicus</i>	NW Atlantic, Greenland, Disko Bugt	year	0.1-0.2 (d)	Petersen (1978)
<i>Sphenia binghami</i>	NE Atlantic, England, Bristol Channel	year	0.45	George and Warwick (1985)
<i>Spisula elliptica</i>	NE Atlantic, England, Swansea Bay	year	1.65	Warwick and George (1980)
<i>Tagelus divisus</i>	NW Atlantic, USA, Biscayne Bay	year	1.55	Moore (1972)
<i>Tellina fabula</i>	NE Atlantic, England, Carmarthen Bay	year	0.90	Warwick, George and Davies (1978)
<i>Tellina fabula</i>	North Sea, Germany, German Bight	year	0.9-1.7 (a)	Salzwedel (1980)

Table 2. - P/B ratios of macro-endofauna (11).

Mollusca - Bivalvia (cont.)

Tellina martinicensis	NW Atlantic, USA, Biscayne Bay	year	2.40	Moore (1972)
Venerupis aurea	Engl.Channel, England, Southampton	year	1.10	Hibbert (1976)
Venerupis pullastra	NE Atlantic, Norway, Seljehölen	year	0.15	Johannessen (1973)
Venus striatula	NE Atlantic, England, Carmarthen Bay	year	0.40	Warwick, George and Davies (1978)
Yoldia limatula	NW Atlantic, USA, Long Island	year	2.30	Sanders (1956) in Greze (1978)

Priapulida

Halicryptus spinulosus	Baltic Sea, Germany, Kiel Bay	year	0.90	(h)	Arntz (1971)
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- (a) gonadal production included
- (b) gonadal production excluded
- (c) different years
- (d) different locations
- (e) different years and locations

- (f) different age groups
- (g) 0-group or juveniles only
- (h) minimal estimates of production and P/B ratio
- (i) real P/B ratio presumed to be considerably lower

Single P/B ratios, given together with ranges, are averages for all years, locations or age-groups